## THE DYNAMICS OF A FLUCTUATING GROWTH RATE[1]

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Quantitative studies of growth phenomena should lead to a considera-
tion of the energy relationships involved. We cannot but believe, in the
absence of contrary evidence, that the life processes of living organisms
are manifestations of the same principles of energy relationships which
exist in other parts of the universe. The study of these energy relation-
ships ought not, therefore, to be disregarded. Our aspirations for such
knowledge, which have received so much encouragement from the dis-
covery of the principle of the conservation of energy, can never be entirely
suppressed.

This quantitative study of the rate of growth of shoots on a perennial
plant, has been attempted in order to gain an insight into some kinetic
aspects of the problem of growth. Growth, in one form or another, is
the end product of most of the energy transformations of a tree. Not all
forms of growth are readily measured. Increase in length is the most
readily measured and its determination is fairly free from error. Increase
in weight might be better, but where one wishes to study identical shoots
through the season, weighing is impossible because it requires removal of
the shoots from the tree.

The present study is based upon measurements of 70 selected shoots
of Royal apricot trees which grew on the grounds of the Citrus Experi-
ment Station at Riverside, California. The observations were made
during the growing season of 1918. At the time the observations began,
the trees had been growing two years in the orchard. The trees on which
shoots were selected for measurement were scattered over the entire
orchard in such a way that a fairly random distribution was obtained.

Shortly after the new shoots appeared, two were selected on each tree
which had been pruned according to the "Winter-vase" type (a tree which
is pruned every winter to produce a vase type). The type of pruning

397

was thus uniform, and since the trees were periodically irrigated throughout the season, it is believed that conditions necessary for fairly uniform growth were afforded. The trees, being so young, produced no fruit and consequently growth was not influenced by that activity. The selected shoots were marked with a line of India ink ten centimeters from the growing point and all measurements were made from this as a base line.

Most of the shoots produced several lateral branches during the season. The length of these laterals was disregarded as far as these studies are concerned. The propriety of this procedure may be questioned, yet it is difficult to see any valid objection thereto, because in measuring the increase in length of a growing shoot we are measuring the catalytic activity of a group of meristematic cells in the apical bud of that shoot. Unless the lateral branches of a shoot have some modifying effect either upon the growth catalyst, or upon the supply of material upon which the catalyst acts, it is difficult to see how the presence of the lateral shoots can modify the growth rate of the main branch. Since we know that removal of the lateral branches of a shoot retards rather than accelerates the length-growth of the main shoot, we are not warranted in assuming that their presence has a retarding influence upon the growth of the main shoot.

*The Course of Growth of the Apricot Shoots.*[2]—If the growth of a branch is similar in its rate to some form of autocatalytic reaction, we should expect the length of the branches to be determined by some sort of a unimolecular reaction formula which shall involve the time and a growth constant.

The most generally useful equation to express this sort of a rate is that of autocatalysis,

$$dx/dt = kx(a-x) \qquad (1)$$

in which $a$ represents the final size of the plant, $x$ is the height (or size) at any time, $t$, and $k$ is the velocity constant of the reaction. A paper recently published (Reed and Holland, 1919) has shown that the growth rate of Helianthus is well expressed by this equation, but it does not necessarily follow that the growth rate of individual shoots on a perennial tree will follow the same type of growth as the axis of an annual plant like the sunflower.

Inspection of the observed values shows that there were three quite distinct cycles of growth in the growing season. The existence of these cycles may be seen by inspection of the graph in figure 1, but better by the observed increments in table 4. The large weekly increments in the first few weeks of the season diminish to a minimum value at the 9th week; then for a few weeks are larger, diminishing again to the 18th week; they increase to the 21st week and then decline to the end of the season. The season's growth, therefore, consisted of three cycles of growth each of about 9 weeks duration. These cycles were quite apparent during the

growing season.   At the beginning of each cycle, growth was rapid, the
leaves arising upon that part of the shoot were of maximum size and out-
spread.   As the end of a growth cycle was approached, the slower-growing
portion of the shoot produced smaller and smaller leaves which had more
of a tendency to curl.   Simultaneously, the apical bud of the shoot was
enlarged and became almost completely dormant.   Following the partial
dormancy of the apical bud, lateral shoots were often formed from sub-
apical buds.   However, within a week or two, the next cycle of growth
would start and the shoot would repeat the processes described for the
preceding cycle.

    If the shoots pass through distinct intra-seasonal cycles of growth, we



Time in weeks
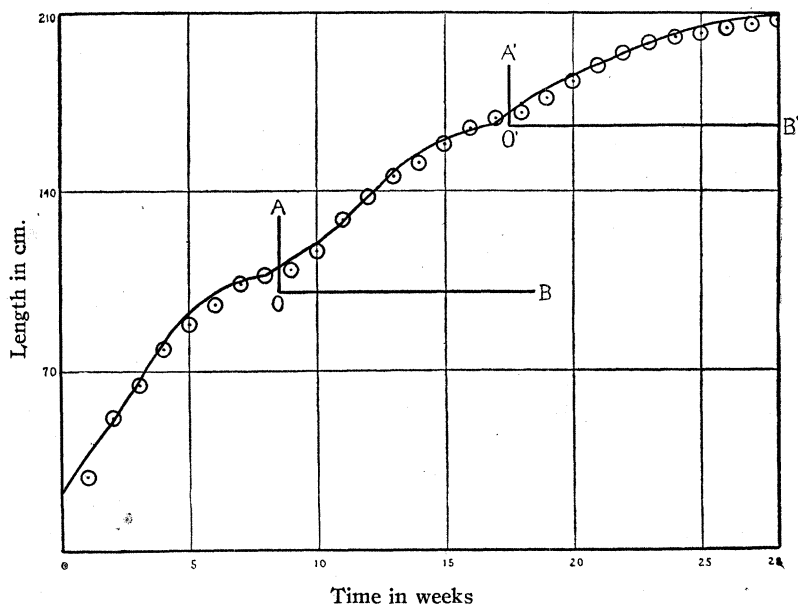
FIG. 1

Growth of apricot shoots represented as three cycles. _____ , curve calcu-
lated from

$$\log \frac{x}{a - x} = k\,(t - t),$$

⊙  ⊙  ⊙  ⊙  , observed values.

should expect that the growth in each cycle should show evidence of being
homogeneous and that it could be expressed definitely.   We may, there-
fore, examine each of the three cycles of growth of the apricot shoots with
this end in view.   From inspection of the data it seems proper to designate
the first cycle as the time from 0 to 8 weeks, the second from 9 to 17
weeks, and the third from 18 to 28 weeks.   If each of these follows the
course of a more or less independent autocatalytic reaction, we may
compute their growth by the formula

$$\log \frac{x}{a - x} = K \, (t - t_1) \tag{2}$$

which is the integral form of the equation (1), in which $a$ is the length of the shoot at the end of the cycle, $x$ is the length at any given time, $t$, $K = ak$, and $t_1$ is the time at which the cycle is half completed, i.e., when $x = a/2$.

The computations may be followed by the aid of table 1. Since the new shoots were marked at the commencement of observations at a uniform distance of 10 cm. from the tip, we may take the value of $x$ as 10 when $t = 0$. The successive length of shoots in each cycle was computed from the equation (2). For convenience the time was computed in days instead of weeks. Data for the three cycles are given in table 1.

For the computation of the second and third cycles the axes were moved to AOB and A′O′B′ (fig. 1). For the second cycle the observed values of $x$ are diminished by 100 cm. and for the third cycle by 165 cm. Having obtained the mean value of $K$ for each cycle, the calculated values of $x$ were obtained from the equation stated above.

The observed and calculated values of this kind of a reaction are apt to show more divergence in the initial stages than after the reaction gets under way. The growth rate is apparently no exception to this rule. However, the divergence is not excessive when one considers the nature of the material and the observational errors involved in making measurements. The graph in figure 1 shows the nature of the curves and their agreement with observed values. It is thus apparent, not only that the growth process followed the course of a definite reaction, but that the individual cycles which made up the growth period also follow a definite course which conforms to certain quantitative relationships.

It will be noted that there is very good agreement between the observed and computed values of these three cycles and that each in itself appears to follow the course of an autocatalytic reaction. The root-mean-square deviations of the values of the three cycles are 5.15 cm., 2.15 cm., and 2.52 cm.

It will be further noted that the mean value of $K$ in the three cycles is successively less in each case, being, 0.0380, 0.0355, and 0.0277 respectively. Reference to the graph in figure 1 shows that the mean slope of the three curves is also successively less.

This analysis of the growth rate of the apricot shoots is taken to indicate that their seasonal growth was made up of three distinct cycles of approximately 9 weeks each. In the first cycle growth was more rapid than in any other. Growth goes on at a more rapid rate during approximately the first third of each cycle and then "fades away" toward the end of that cycle.

While this analysis affords some interesting insight into the growth

TABLE 1

GROWTH RATE OF APRICOT SHOOTS, CALCULATED UPON THE BASIS OF THREE CYCLES IN THE GROWING SEASON

| | 1ST CYCLE | | | | 2ND CYCLE | | | | 3RD CYCLE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $t$ DAYS | $x$ (OBSERVED) (CM.) | $K$ | $x$ (CALC.) (CM.) | $\theta$ (CM.) | $t$ DAYS | $x$ (OBSERVED) (CM.) | $K$ | $x$ (CALC.) (CM.) | $\theta$ | $t$ DAYS | $x$ (OBSERVED) (CM.) | $K$ | $x$ (CALC.) | $\theta$ (CM.) |

| $t$ DAYS | $x$ (OBS.) | $K$ | $x$ (CALC.) | $\theta$ | $t$ DAYS | $x$ (OBS.) | $K$ | $x$ (CALC.) | $\theta$ | $t$ DAYS | $x$ (OBS.) | $K$ | $x$ (CALC.) | $\theta$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 10.0 | 0.0625 | 21.9 | 11.9 | 64 | 9.6 | 0.0419 | 12.2 | 2.6 | 126 | 5.3 | 0.0464 | 10.5 | 5.2 |
| 7 | 28.5* | 0.0510 | 34.4 | 5.9 | 70 | 16.7 | 0.0418 | 19.0 | 2.3 | 133 | 11.8 | 0.0383 | 14.5 | 2.7 |
| 14 | 51.5 | 0.0295 | 50.2 | −1.3 | 77 | 28.5 | 0.0320 | 27.8 | −0.7 | 140 | 18.4* | 0.0347 | 19.2 | 0.8 |
| 21 | 64.5 | 0.0294 | 67.1 | 2.6 | 84 | 37.4 | 0.0320 | 37.7 | 0.3 | 147 | 24.4 | 0.0285 | 24.4 | 0.0 |
| 28 | 78.6 | 0.0328 | 81.8 | 3.2 | 91 | 45.3* | 0.0300 | 47.2 | 1.9 | 154 | 29.2 | 0.0273 | 29.3 | 0.1 |
| 35 | 88.0 | 0.0313 | 92.8 | 4.8 | 98 | 50.8 | 0.0269 | 54.9 | 4.1 | 161 | 33.0 | 0.0258 | 33.7 | 0.7 |
| 42 | 95.6 | 0.0310 | 100.1 | 4.5 | 105 | 58.4 | 0.0310 | 60.5 | 2.1 | 168 | 35.1 | 0.0224 | 37.2 | 2.1 |
| 49 | 103.9 | 0.0365 | 104.5 | 0.6 | 112 | 64.8 | 0.0374 | 64.2 | −0.6 | 175 | 36.9 | 0.0206 | 39.9 | 3.0 |
| 56 | 107.2 | 0.0381 | 107.2 | 0.0 | 119 | 68.4 | 0.0463 | 66.5 | −1.9 | 182 | 38.8 | 0.0201 | 41.9 | 3.1 |
| | | | | | | | | | | 189 | 40.6 | 0.0203 | 43.2 | 2.6 |
| | | | | | | | | | | 196 | 42.0 | 0.0205 | 44.1 | 2.1 |

Assumed value of $a$ = 110.4

Assumed value of $t_1$ = 16.0

Mean value of $K$ = 0.0380

Root-mean-square deviation of observed from calculated values of $x$ = 5.15 cm.

Assumed value of $a$ = 69.7

Assumed value of $t_1$ = 82.0

Mean value of $K$ = 0.0355

Root-mean-square deviation of observed from calculated values of $x$ = 2.15 cm.

Assumed value of $a$ = 45.8

Assumed value of $t_1$ = 145.0

Mean value of $K$ = 0.0277

Root-mean-square deviation of observed from calculated values of $x$ = 2.52 cm.

* Interpolated.

rate of the apricot shoots it is not entirely satisfactory to dissect thus a process which is undoubtedly homogeneous in its nature. Our efforts must continually bend toward the problem of explaining the organism and its activities as a whole. We shall, therefore, attempt to study the dynamics of the entire season's growth and to learn something about the nature of the process.

Wilhelmy's equation, which has been found to apply to many processes in physical chemistry, was used;

$$\frac{dx}{dt} = k\,(a-x) \tag{3}$$

TABLE 2

CALCULATED AND OBSERVED LENGTH OF APRICOT BRANCHES

| TIME WEEKS | OBSERVED CM. | CALCULATED FROM $x=210\ (1 - e^{-0.095t})$ CM. | $\theta$ |
|---|---|---|---|
| 1 | 15.8 | 19.1 | − 3.3 |
| 2 | 41.5 | 36.3 | − 5.2 |
| 3 | 54.5 | 52.1 | + 2.4 |
| 4 | 68.6 | 66.4 | + 2.2 |
| 5 | 78.0 | 79.4 | − 1.4 |
| 6 | 85.6 | 91.4 | − 5.8 |
| 7 | 93.9 | 102.0 | − 8.1 |
| 8 | 97.2 | 111.8 | −14.6 |
| 9 | 99.6 | 120.8 | −21.2 |
| 10 | 106.7 | 128.8 | −22.1 |
| 11 | 118.5 | 136.0 | −17.5 |
| 12 | 127.4 | 142.8 | −15.4 |
| 13 | 135.3 | 148.8 | −13.5 |
| 14 | 140.8 | 154.7 | −13.9 |
| 15 | 148.4 | 159.5 | −11.1 |
| 16 | 154.8 | 164.0 | − 9.2 |
| 17 | 158.4 | 168.1 | − 9.7 |
| 18 | 161.3 | 172.0 | −10.7 |
| 19 | 166.8 | 175.6 | − 8.8 |
| 20 | 173.4 | 178.8 | − 5.4 |
| 21 | 179.4 | 181.2 | − 1.8 |
| 22 | 184.2 | 184.0 | 0.2 |
| 23 | 188.0 | 186.5 | 1.5 |
| 24 | 190.1 | 188.6 | 1.5 |
| 25 | 191.9 | 190.4 | 1.5 |
| 26 | 193.8 | 192.2 | 1.6 |
| 27 | 195.6 | 193.8 | 1.8 |
| 28 | 197.0 | 195.2 | 1.8 |

where $x$ represents the length of the shoot at time $t$, $a$ represents the final length, and $k$ is a constant of the reaction.

By integrating the above equation, we get

$$x = a\,(1 - e^{-kt}) \qquad\qquad (4)$$

in which $e$ is the base of the natural logarithms.

It is of interest to know whether the measurements of the apricot shoots will approximate values which will be given by the above equation. Reference to table 2, shows that the final mean length of the shoots was 197 cm.   Let us assume that the limiting value of $x$ is 210.   Let this be

TABLE 3

LENGTH OF APRICOT SHOOTS AT WEEKLY INTERVALS DURING THE GROWING SEASON.
VALUES OBSERVED AND CALCULATED FROM EQUATION (1)

| $t$ | $x$ OBSERVED | $\{210[1 - e^{-.095(t-1)}]\}_1$ | $\{19.1\,e^{-.055t}\cos\frac{\pi}{14}\}_2$ | $x$ CALCULATED $\{\}_1 + \}_2$ | $\theta$ |
|---|---|---|---|---|---|
| 0 | 0 | − 19.1 | 19.1 | 0 | 0 |
| 1 | 15.8 | 0 | 17.6 | 17.6 | −1.8 |
| 2 | 41.5 | 19.1 | 15.4 | 34.5 | 7.0 |
| 3 | 54.5 | 36.3 | 12.7 | 49.0 | 5.5 |
| 4 | 68.6 | 52.1 | 9.5 | 61.6 | 7.0 |
| 5 | 78.0 | 66.4 | 6.3 | 72.7 | 5.3 |
| 6 | 85.6 | 79.4 | 3.0 | 82.4 | 3.2 |
| 7 | 93.9 | 91.4 | 0 | 91.4 | 2.5 |
| 8 | 97.2 | 102.0 | −2.7 | 99.3 | −2.1 |
| 9 | 99.6 | 111.8 | −5.0 | 106.8 | −7.2 |
| 10 | 106.7 | 120.8 | −6.8 | 114.0 | −7.3 |
| 11 | 118.5 | 128.8 | −8.1 | 120.7 | −2.2 |
| 12 | 127.4 | 136.0 | −8.9 | 127.1 | 0.3 |
| 13 | 135.3 | 142.8 | −9.1 | 133.7 | 1.6 |
| 14 | 140.8 | 148.8 | −8.8 | 140.8 | 0.8 |
| 15 | 148.4 | 154.7 | −8.1 | 146.6 | 1.8 |
| 16 | 154.8 | 159.5 | −7.1 | 152.4 | 2.4 |
| 17 | 158.4 | 164.0 | −5.9 | 158.1 | 0.3 |
| 18 | 161.3 | 168.1 | −4.4 | 163.7 | −2.4 |
| 19 | 166.8 | 172.0 | −2.9 | 169.1 | −2.3 |
| 20 | 173.4 | 175.6 | −1.4 | 174.2 | −0.8 |
| 21 | 179.4 | 178.8 | 0 | 178.8 | 0.6 |
| 22 | 184.2 | 181.2 | 1.3 | 182.5 | 1.7 |
| 23 | 188.0 | 184.0 | 2.3 | 186.3 | 1.7 |
| 24 | 190.1 | 186.5 | 3.2 | 189.7 | 0.4 |
| 25 | 191.9 | 188.6 | 3.8 | 192.4 | −0.4 |
| 26 | 193.8 | 190.4 | 4.1 | 194.5 | −0.7 |
| 27 | 195.6 | 192.2 | 4.2 | 196.4 | −0.8 |
| 28 | 197.0 | 193.8 | 4.1 | 197.9 | −0.9 |

taken as the value of $a$. By a series of approximations it was found that the value of $k$ is near 0.095. We may then write:

$$x = 210 \ (1 - e^{-.095t}) \tag{5}$$

The values of $x$ corresponding to values of $t$ were determined and are given in table 2, together with the observed length of the shoots.

While there is a general harmony between the calculated and observed length of the branches at the weekly intervals, the values are not sufficiently close to be satisfactory. An examination of the figures shows that during the first seven weeks the computed length of the branches is fairly correct; from the 8th to the 20th week the computed values are too large; from the 20th week to the end of the season, the two sets of values agree fairly well.

The formula appears to fit the growth in the initial and latter part of the season, but growth lags behind the calculated values from the 8th to the 20th weeks.

This leads us to consider the possibility that the length-growth of these apricot branches follows the course of a reaction which consists of two consecutive unimolecular reactions, one of which at first accelerates and later retards the other. (The dynamics of such reactions have been discussed by Mellor, _Chemical Statics and Dynamics_ (1914).) It is, therefore, necessary to increase the previously obtained values of $x$ by some quantity which will be large when $t$ is small and which will be comparatively small when $t$ is large.

The nature of this quantity was ascertained by shifting all the values of $t$ toward the ordinate, which was done by substituting $t - 1$ for $t$ in each case. The values by which the resulting determinations differed from the observed values were then computed and the differences were found to be periodically alternately positive and negative. (Compare columns 2 and 3 in table 3.) An appropriate form expressing these fluctuating differences may be a function of $t$ involving the cosine. This will equal 1 when the value of the angle is 0, will decrease as the angle increases, then be negative as the angle increases from 90° to 270°, and become positive again in the last quadrant. By trial it was found that the difference between the observed values and those of the exponential function could be approximately expressed by

$$19.1 \ [e^{-.055t} \cos \frac{\pi}{14} t]$$

The equation as used was then

$$x = 210 \ [1 - e^{.095 \ (t - 1)}] + 19.1 \ [e^{-.055t} \cos \frac{\pi}{14} t] \tag{6}$$

The values of $x$ corresponding to the time intervals from 0 to 28 are given in the fifth column of table 3. The root-mean-square deviation

$(\Sigma d^2/n)^{1/2}$ of these results is 3.4 cm.    The agreement, therefore, is satisfactory.

Comparing the calculated values of $x$ with the observed, it will be seen that there are 16 deviations on the $+$ side and 12 deviations on the $-$ side.    In figure 2, the upper curve shows the calculated course of the growth process alongside of the actual observed values.

The writer is fully aware that equation (6) is somewhat cumbersome. Its claim for consideration is, however, an important one, viz., it satisfactorily represents the observed facts.    In the present state of our knowledge it seems advisable to use a formula like the above rather than a simpler type which might not so accurately represent the actual growth
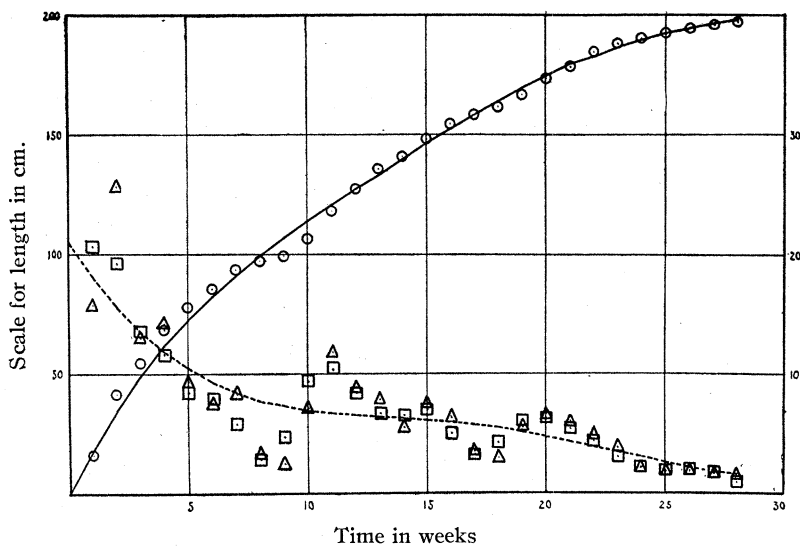


Time in weeks

FIG. 2

Growth of apricot shoots. ——————— curve calculated from

$$x = 210[1 - e^{-.095\,(t-1)}] + 19.1\,[e^{-.055t}\cos\frac{\pi}{14}t]$$

— — — — — — — curve calculated from

$$\frac{dx}{dt} = 19.95\,e^{-.095\,(t-1)} - 19.1\,e^{-.055t}(0.055\cos\frac{\pi}{14}t + \frac{\pi}{14}\sin\frac{\pi}{14}t)$$

⊙  ⊙  ⊙, observed lengths of shoots.
△  △  △, observed increments of shoots.
⊡  ⊡  ⊡, "adjusted values" (S).

reaction.    Future studies may show that a satisfactory equation of simpler form exists.

A consideration of equation (6) shows that we are here dealing with a homogeneous reaction, consisting of two unimolecular reactions, the first of which is always positive, and the second alternately positive and negative.

Putting this into terms of the tree, we may say that the growth of the apricot branches was, in the first 6 weeks, accelerated by amounts which diminished from 19.1 cm. at the outset to 3.0 cm. in the 6th week. From the 7th to the 21st week the growth was retarded by regularly varying amounts, and from then on, there was an acceleration, amounting at the most, to 4.2 cm.

*The Dynamical Basis for Growth.*—Our attention next passes to the question of the rate of growth. Since equation (6) represents the length of the apricot branches at successive intervals, we should obtain an equation by differentiating it, which will represent the rate at which they grow. Clearly, this relationship is of considerable physiological importance. By differentiating equation (6) we obtain the following

$$\frac{dx}{dt} = 19.95 \, [e^{-.095 \, (t-1)}] - 19.1 \, [e^{-.055t} \, (.055 \, \cos \frac{\pi}{14} t + \frac{\pi}{14} \sin \frac{\pi}{14} t)] \quad (7)$$

This expression will be more easily grasped if we obtain the values of the equation which correspond to different values of $t$ and compare them with the rate per week (increments) actually observed as shown in table 4. The dotted line in figure 2 shows the graph obtained by plotting these values along with the observed values of the increments for the same intervals. The agreement between the two is good, with few exceptions. Better agreement might have been obtained had there been more frequent observations during the first two weeks; as it is, the number of observa-

TABLE 4

VALUES OF THE WEEKLY INCREMENTS IN LENGTH OF APRICOT BRANCHES, COMPARED
WITH THE RATE OF GROWTH CALCULATED FROM THE FORMULA

$$\frac{dx}{dt} = 19.95[e^{-.095 \, (t-1)}] - 19.1[e^{-.055t}(.055 \, \cos \frac{\pi}{14} t + \frac{\pi}{14} \sin \frac{\pi}{14} t)]$$

| $t$ | OBSERVED CM. | CALCULATED CM. | $\theta$ | $t$ | OBSERVED CM. | CALCULATED CM. | $\theta$ |
|---|---|---|---|---|---|---|---|
| 0 | | 20.9 | | 15 | 7.6 | 6.1 | 1.5 |
| 1 | 15.8 | 18.1 | −2.3 | 16 | 6.4 | 6.0 | 0.4 |
| 2 | 25.7 | 15.6 | 10.1 | 17 | 3.6 | 5.7 | −2.1 |
| 3 | 13.0 | 13.5 | −0.5 | 18 | 2.9 | 5.4 | −2.5 |
| 4 | 14.1 | 11.8 | 2.3 | 19 | 5.5 | 5.1 | 0.4 |
| 5 | 9.4 | 10.4 | −1.0 | 20 | 6.6 | 4.7 | 1.9 |
| 6 | 7.6 | 9.3 | −1.7 | 21 | 6.0 | 4.3 | 1.7 |
| 7 | 8.3 | 8.4 | −0.1 | 22 | 4.8 | 3.9 | 0.9 |
| 8 | 3.3 | 7.7 | −4.4 | 23 | 3.8 | 3.4 | 0.4 |
| 9 | 2.4 | 7.3 | −4.9 | 24 | 2.1 | 3.0 | −0.9 |
| 10 | 7.1 | 6.9 | 0.2 | 25 | 1.8 | 2.5 | −0.7 |
| 11 | 11.8 | 6.7 | 5.1 | 26 | 1.9 | 2.1 | −0.2 |
| 12 | 8.9 | 6.6 | 2.3 | 27 | 1.8 | 1.7 | 0.1 |
| 13 | 7.9 | 6.4 | 1.5 | 28 | 1.4 | 1.5 | −0.1 |
| 14 | 5.5 | 6.3 | −0.8 | | | | |

tions in the early part of the growth period are too scanty to give suffi-
cient data for more accurate determinations.   It will be noted that half
of the observed values lie above the graph and half below it.   This gives
confidence in the reliability of the calculated values.   The root-mean-
square deviation of the 28 values is 2.78 cm.

Table 5 gives the values of $S$ in comparison with the computed values
of $dx/dt$.   $S$ is computed from

$^1/_2$ [observed length at time $(t + 1)$ − observed length at time $(t-1)$].

TABLE 5

VALUES OF S COMPUTED FROM $^1/_2$ [(OBS. LENGTH AT TIME $t + 1$) − (OBS. LENGTH AT
TIME $t − 1$)] AND VALUES OF $\dfrac{dx}{dt}$.

| $t$ | $S$ | $\frac{dx}{dt}$ | $\theta$ | $t$ | $S$ | $\frac{dx}{dt}$ | $\theta$ |
|---|---|---|---|---|---|---|---|
| 1 | 20.7 | 18.1 | −2.6 | 15 | 7.0 | 6.1 | −0.9 |
| 2 | 19.3 | 15.6 | −3.7 | 16 | 5.0 | 6.0 | 1.0 |
| 3 | 13.5 | 13.5 | 0.0 | 17 | 3.2 | 5.7 | 2.5 |
| 4 | 11.7 | 11.8 | 0.1 | 18 | 4.2 | 5.4 | 1.2 |
| 5 | 8.5 | 10.4 | 1.9 | 19 | 6.0 | 5.1 | −0.9 |
| 6 | 8.0 | 9.3 | 1.3 | 20 | 6.3 | 4.7 | −1.6 |
| 7 | 5.8 | 8.4 | 2.6 | 21 | 5.4 | 4.3 | −1.1 |
| 8 | 2.8 | 7.7 | 4.9 | 22 | 4.3 | 3.9 | −0.4 |
| 9 | 4.7 | 7.3 | 2.6 | 23 | 3.0 | 3.4 | 0.4 |
| 10 | 9.4 | 6.9 | −2.5 | 24 | 2.0 | 3.0 | 1.0 |
| 11 | 10.3 | 6.7 | −3.6 | 25 | 1.8 | 2.5 | 0.7 |
| 12 | 8.4 | 6.6 | −1.8 | 26 | 1.8 | 2.1 | 0.3 |
| 13 | 6.7 | 6.4 | −0.3 | 27 | 1.6 | 1.7 | 0.1 |
| 14 | 6.5 | 6.3 | −0.2 | 28 | 0.7 | 1.5 | 0.8 |

If we use the values $(S)$ which represent the slope of the chord whose
mid-point corresponds to time, $t$, we shall obviate the minor fluctuations
and get a more comparable expression of the observed rate of growth.
McEwen and Michael (1919) have pointed out the usefulness of this
method (p. 111) which depends upon the fact that the slope of the chord
of a simple curve is approximately equal to that of the tangent at the
point midway between the extremities of the chord.   The root-mean-
square deviations of these values is only 1.91 cm., which indicates a
satisfactory agreement.

When these computations are translated into terms of the growing
tree it appears that the growth rate in the early part of the season is high,
but that it declines as the season advances.   The rate of growth of the
apricot branches indicates that the growth-impelling agency is at a maxi-
mum at the beginning of the season and that it diminishes as growth
proceeds.   In the first seven or eight weeks the growth rate declines more
rapidly than in any other period.   From the eighth to the nineteenth

week the rate is fairly constant, only diminishing about 2.5 cm., but from that time on, the decline is considerably more rapid. At the end of the growing season the rate is less than one-tenth of the initial rate.

From a biological point of view, our interest in any equation representing the growth of organisms is not confined to evolving equations which shall represent their size at any given time. If we know the rate at which an organism grows and can express it quantitatively, we are in a position to analyze the processes by which it increases in size.

To facilitate matters, we may write equation (6) in a general form

$$x = a \, [1 - e^{-k_1(t-1)}] + b e^{-k_2 t} \cos \alpha t.$$

When differentiated, this becomes

$$\frac{dx}{dt} = a k_1 e^{-k_1 (t-1)} - b e^{-k_2 t} \{ k_2 \cos \alpha t + \alpha \sin \alpha t \}$$

which is the general form corresponding to equation (7). This can also be written in the form

$$\frac{dx}{dt} = k_1 \left[ (a-x) + \frac{-b e^{-k_2 t} \{ (k_2 - k_1) \cos \alpha t + \alpha \sin \alpha t \}}{k_1} \right]$$

For the sake of brevity let

$$Y = -b e^{-k_2 t} [(k_2 - k_1) \cos \alpha t + \alpha \sin \alpha t]$$

We may then write

$$\frac{dx}{dt} = k_1 [(a-x) + Y/k_1]. \dots \dots \dots \dots \dots \quad (8)$$

In the case of the apricot data

$$Y = 19.1 \, e^{-.055t} \left\{ -.04 \, \cos \frac{\pi}{14} t + \frac{\pi}{14} \sin \frac{\pi}{14} t \right\}.$$

The advantage of this form of expression lies in the fact that $Y$ may be expressed in terms of $x$, since equation (7) may be written

$$Y = \frac{dx}{dt} - k_1 (a-x).$$

It seems, therefore, that the growth of these apricot shoots in one season conforms to that of a unimolecular consecutive reaction, in which the main reaction is influenced by a secondary reaction product. The rate of the main reaction would follow the path of curve $A$ in figure 3, if it were alone operative. The secondary reaction (represented by curve $B$) has an additive effect on the main reaction and gives the resultant course shown by curve $C$. In the first part of the season, $B$ has a negative value, its effect, therefore, is to diminish $A$. In the latter part of the season, $B$ has positive values and accordingly augments $A$.

The writer is inclined to adopt the suggestion of Robertson (1913) concerning the progressive increase or decrease in the amount of growth-catalyst during a cycle. If we assume that in this sort of a reaction the

amount of catalyst is in some way proportional to values of $dx/dt$, there would be in the present instance a progressive decrease during the growing season. If the initial excess of catalyst is unfavorable to growth then the effect of $Y$ (which is negative during the first part of the season) would accelerate the reaction because it operates to cause a more rapid decrease in the amount of the catalyst. The amount of this acceleration is actually indicated by the values of 19.1 $[e^{-.055t}$ cos $\pi/14]$ in equation (6).

If the assumptions made in this study have any basis, it would seem that some light has been thrown upon the process of growth. It appears that growth proceeds at a definite rate, and is capable of mathematical expression. The growth rate appears to be proportional to the amount
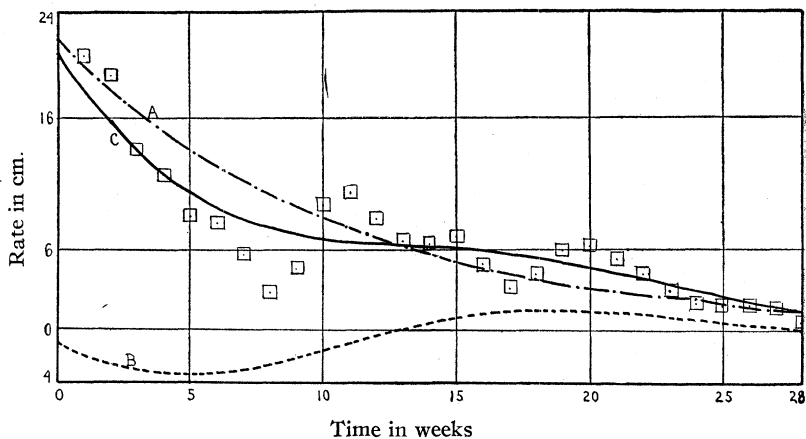


Time in weeks

FIG 3

Growth rate of apricot shoots.

—.—.—, (A), curve calculated from $ake^{-k_1 (t - 1)}$

— — —, (B), curve calculated from $-be^{-k_2t} [k_2 \cos \alpha t + \alpha \sin \alpha t]$

————, (C), curve calculated from sum of values of (A) and (B).

▣   ▣   ▣   observed increments.

of a hypothetical catalyst and the intra-seasonal cycles of growth may be indicative of fluctuations in the amount of active catalyst in the organism.

*Summary.*—1. The growth of shoots on a selected sample of young apricot trees, followed a definite, though fluctuating rate. The maximum growth rate was exhibited soon after the growth of the season began, and declined with some regularity to the end of the season, though three distinct intra-seasonal cycles of growth were apparent.

2. The growth in each cycle closely resembled the rate of an autocatalytic reaction. The growth rate for the entire season conforms to that of a reaction consisting of two unimolecular reactions, one of which at first accelerates and subsequently retards the other.

3. If growth be assumed to be proportional to the amount of active catalyst present, a method is available for studying the dynamics of the growth process.

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# ANALYTICAL NOTE ON CERTAIN RHYTHMIC RELATIONS IN ORGANIC SYSTEMS

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Periodic phenomena play an important rôle in nature, both organic and inorganic.

In chemical reactions rhythmic effects have been observed experimentally, and have also been shown, by the writer[1] and others,[2] to follow, under certain conditions, from the laws of chemical dynamics.

However, in the cases hitherto considered on the basis of chemical dynamics, the oscillations were found to be of the damped kind, and therefore, only transitory (unlike certain experimentally observed periodic reactions). Furthermore, in a much more general investigation by the writer, covering the kinetics not only of chemical but also of biological systems, it appeared, from the nature of the solution obtained, improbable[3] that undamped, permanent oscillations would arise in the absence of geometrical, structural causes,.in the very comprehensive class of systems considered. For it seemed that the occurrence of such permanent oscillations, the occurrence of purely imaginary exponents in the exponential series solution presented, would demand peculiar and very specific relations between the characteristic constants of the systems undergoing transformation; whereas in nature these constants would, presumably, stand in random relation.

It was, therefore, with considerable surprise that the writer, on applying his method to certain special cases, found these to lead to undamped, and hence indefinitely continued, oscillations.

As the matter presents several features of interest, and illustrates certain methods and principles, it appears worth while to set forth the argument and conclusions here.